Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 128, No. 9

THE LARGER EMBOLOMEROUS AMPHIBIANS OF THE AMERICAN CARBONIFEROUS

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With Two Plates

CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

February, 1963

Bull. Mus. Comp. Zool., Harvard Univ., 128(9): 415-454, Feb. 1963

No. 9 — *The Larger Embolomerous Amphibians of the American Carboniferous*

By

Alfred Sherwood Romer

1. A Large Embolomere Skull from the Conemaugh Series of Ohio.

Notable in the vertebrate fauna of the Upper Carboniferous of Great Britain is the presence of numerous specimens of large embolomerous amphibians. Remains of this sort, commonly described as *Pteroplax* or *Eogyrinus*, are especially abundant in the coal shales of the Newsham Main Seam near Newcastle-upon-Tyne; the original descriptions were given in a series of papers by Hancock and Atthey, and reviewed by Watson in his important Croonian lecture of 1926 on the Evolution and Origin of the Amphibia.

In North America, however, remains of large Carboniferous embolomeres are rare.[1] In the present paper I shall describe the recently discovered skull of a large embolomere comparable to the familiar British forms, and take the opportunity to review other American remains which may pertain to large Carboniferous embolomeres. For the privilege of describing this skull I am indebted to the authorities of the U. S. National Museum, including Dr. C. Lewis Gazin, Curator of Vertebrate Paleontology, and Associate Curator David H. Dunkle. I am indebted to Dr. Donald Baird for aid and advice, and to the National Science Foundation for aid in the collection and preparation of Carboniferous materials, including partial preparation of the skull under consideration.

A few years ago the Pennsylvania Railroad was engaged in improving its main Pittsburgh-St. Louis line west of Steubenville, Ohio. About ten miles directly west of that city a deep cut was excavated north of the village of Bloomingdale, Wayne Township, Jefferson County, Ohio. In the process of excavation, by bulldozer and drag lines, remains of the skull and jaws of a large amphibian were unearthed near the top of the cut. The locality, in terms of federal land surveys, is SW 1/4 SE 1/4 SE 1/4, Section

[1] Under the assumption then prevalent that all Carboniferous labyrinthodonts were embolomeres, I assigned, in 1930, a considerable number of specimens from the famous Linton coal mine to this labyrinthodont order; however, Dr. Donald Baird, who has in process a thorough revision of the Linton fauna, finds that a good fraction of these materials are those of temnospondyls rather than embolomeres.

24, Wayne Township. The site is 180 feet northeast of the northeast abutment of an overpass bridge and 20 feet above a spring which drains into the side of the cut. The geology of this area has been described by Lamborn (1930). The shale in which the remains were embedded is 12½ feet above a limestone which is identified as the Ames Limestone, and about 185 feet below the Pittsburgh No. 8 coal. This places it at about the middle of the Conemaugh series of the Pennsylvanian System. It is about 300 feet above the level of the famous Linton amphibian locality (in the northern part of the same county), which is at the Upper Freeport Coal horizon at the summit of the Allegheny series. A modest number of finds of fishes, amphibians, and reptiles have been made from other Conemaugh localities (Romer 1952, p. 105, etc.) but apart from a single centrum mentioned later, no other remains of large embolomeres have been reported. A part of the material was seen and collected, while excavation was in progress, by Dr. Raymond E. Lamborn of the Geological Survey of Ohio; a thorough search made later by Dr. David H. Dunkle of the U.S. National Museum resulted in the discovery of further pieces. The specimen is now catalogued as No. 20636 in the U.S. National Museum collections. From the same horizon were collected several *Platyhystrix*-like amphibian neural spines now being studied by Dr. Peter P. Vaughn; a dozen feet below, at the level of the Ames Limestone, were found several spine fragments of a small *Edaphosaurus,* a small amphibian neural spine, and a few fish teeth including *Cladodus* and a petalodont and part of a cochliodont plate.

Of postcranial remains, there were found only some rib fragments and a few centra and intercentra with diameters of 30 to 35 mm. Presumably the entire skull and jaws were present before excavation; saved from the damage caused by the excavating machinery were broken pieces making up somewhat over half of the skull — mainly the left side — and most of the right jaw ramus. Before the specimen was sent to me for study, it was exhibited as part of a demonstration of the activities of the National Museum before the governing boards of the Smithsonian Institution. For this occasion, the missing parts of the skull and dentition were restored. I am publishing here photographs of the restoration (Pls. 1, 2), despite the fact that various features are open to question, since the illustrations give a much more vivid impression of the skull as it would have appeared in life than the drab factual figures of the parts preserved. It is obvious at once that we are dealing with an animal quite similar to the English embolomeres of the *Pteroplax-Eogyrinus* type; compare, for example, my figures with those of Atthey 1876, plates VIII, IX (*"Anthracosaurus russelli"*) and Atthey 1877, plate XIII.

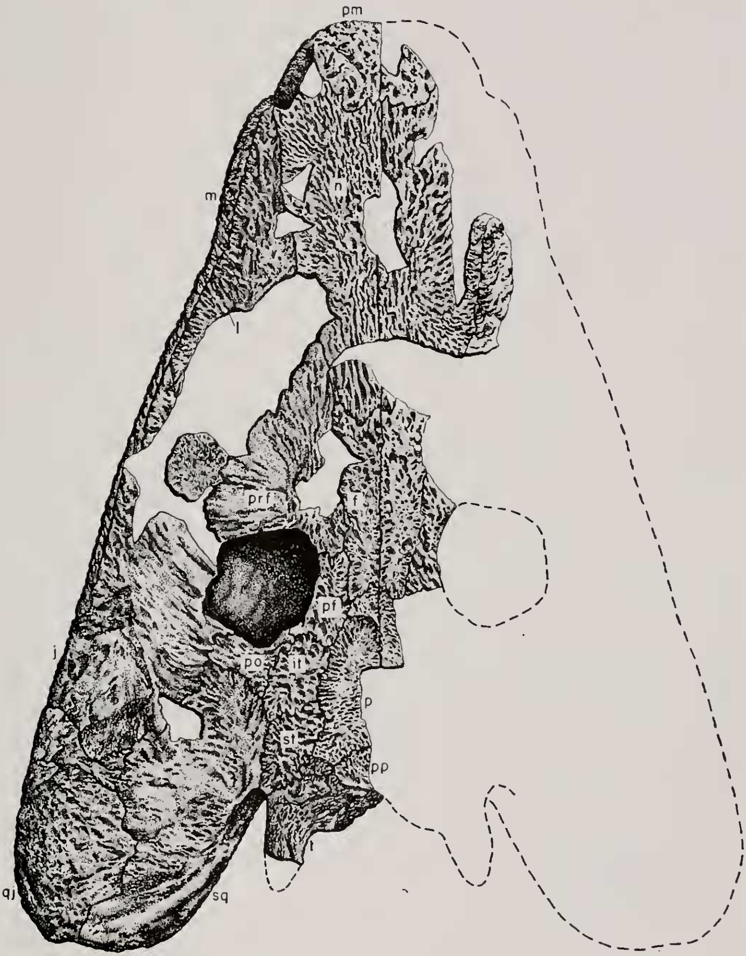

Figure 1. *Neopteroplax conemaughensis.* Skull roof as preserved. x⅓ approximately. Abbreviations: *f*, frontal; *it*, intertemporal; *j*, jugal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *p*, parietal; *pf*, postfrontal; *pm*, premaxilla; *po*, postorbital; *pp*, postparietal; *prf*, prefrontal; *q*, quadrate; *qj*, quadratojugal; *sq*, squamosal; *st*, supratemporal; *t*, tabular.

Skull roof (Figs. 1, 3, 4). Much of the right half of the skull roof was lost beyond recovery during the excavation of the cut. The left side of the skull, however, was nearly completely recovered, as was much of the "snout" region on both sides. On the left, the premaxillary region is slightly imperfect, and a few pieces are missing posteriorly; these are not of great importance except that, unfortunately, areas of the postparietal and parietal close to the midline and including the parietal foramen are absent. The skull had been somewhat crushed dorsoventrally. The length from snout to occiput is 336 mm.; from snout to a line connecting the posterior margins of the quadrates about 395 mm. The *Pteroplax* skull from Newsham described by Atthey in 1876 as "*A. russelli*" is stated to be 13½ inches in length to the occiput, i.e., about 340 mm., very close to the size of the present skull; two figured skull tables from Newsham suggest rather small skulls with lengths of 260-270 mm. The skull proportions are similar to those of *Pteroplax*. There is a moderately long facial region, suggesting piscivorous habits. Crushing has exaggerated the breadth of the cheek region; in life the skull was obviously fairly deep in the quadrate region, the cheeks descending at a considerable angle from the rounded lateral margins of the table. In Figures 3 and 4 the restored skull is seen in dorsal and lateral views, with the effects of crushing eliminated. The width was determined by study of the palatal materials; a latex mold was made of the left half of the roof and fitted over a "form" of modeling clay to find the proper "pitch" of the cheeks.

The sculpture is of a typical labyrinthodont type. It is coarse along the jaw margins, the upper surface of the snout and the table, but relatively smooth over much of the cheek and the region in front of and below the orbit. I find no trace of lateral line canals. Atthey, in the "*A. russelli*" skull, describes a "mucus-groove" along the upper jaws; this appearance, however, may be due (as in the present specimen) to the presence of a marked ridge along the suture between the maxilla and the bones bordering it dorsally.

Determination of sutures is a matter of some difficulty. The animal was obviously mature, and for the most part the sutures between elements are closed. In some instances, as on both sides of the lacrimal anteriorly, the sutures have developed as prominent raised ridges. In nearly every case the approximate boundaries between elements can be defined by study of the radiating pattern of the sculpture of the elements concerned, and the sutures appear to follow low ridges which are not part of the sculpture pattern. In such cases as the contact of jugal and squamosal, where two thin plates of bone are apposed, the breaks due to crushing appear to follow the lines of suture. I have figured a full set of sutures but the reader should be warned that certain of them, at least, are questionable.

The left premaxilla is well preserved, and a fraction of the right element is also present. The bone is thick, forming a rugose rounded terminus to the snout and anteriorly curving downward and somewhat posteriorly to gain the margin of the tooth row. Posterolaterally, it forms half of the margin of the external naris. The maxilla is a very elongate but narrow element. It extends back some 24 cm., tapering in width posteriorly, from the lower margin of the naris to a point below the posterior end of the orbit. Its dorsal contact with the lacrimal is clearly marked off by a raised ridge, and its long suture with the jugal is nearly equally distinct. As in *Pteroplax*, the lacrimal is narrow anteriorly; it enters the posterior margin of the naris for a short distance only. Anteriorly, its suture with the nasal is, like its maxillary contact, a distinct raised ridge. The bone broadens posteriorly, but most of this area of the face is absent in the specimen. With some doubt, I have indicated a short stretch of the supposed jugal contact ventrally and the prefrontal contact dorsally. Obviously in this form, as in *Pteroplax* and *Archeria*, the lacrimal was blocked from entry into the orbital rim by downgrowth of the prefrontal.[1] No evidence of a septomaxilla can be made out in the material.

The left nasal is almost completely preserved, and much of the right is also present. The nasal is a very large element, broad anteriorly where it enters largely into the narial rim, and tapering posteriorly. Anteriorly, there is a distinct, straight, median suture between the two nasals; more posteriorly, the median suture is less certain. The ossification center of the nasal (as indicated by the sculpture pattern) is but about 4.5 cm. back of the front end of the bone, i.e. only about one-third the distance to the frontal suture. In correlation with snout elongation, the posterior portion of the nasal region was a zone of intensive growth, as indicated by the straight longitudinal ridges of the sculpture pattern in this area.

The frontals, almost completely preserved, are of a normal pattern, although somewhat more elongated than in labyrinthodonts with less facial elongation. The fronto-parietal suture is seen on the left side at the expected level.

[1] Dr. Panchen informs me that this appears to be true of *Palaeogyrinus* as well.

Of the parietals, only a small fragment of the right element is present, but the left is almost complete except that, as noted above, the portion of the median border containing the parietal foramen is unfortunately missing. The lateral border is notably concave in outline along the suture with the supratemporal, and the posterior border is similarly concave along the postparietal suture. There is a broad contact with the tabular. The postparietal, as far as preserved, is of normal pattern.

Of the circumorbital elements, the prefrontal is much expanded, as in *Pteroplax,* extending far forward and downward anterior to the orbit, as noted above, excluding the lacrimal from the orbital region. The more dorsal part of the bone is well sculptured; the preorbital plate is nearly smooth and appears to be thin. Little of the anterior and ventral contacts are preserved, although it appears probable that a break seen in the specimen which runs forward from the lower edge of the orbit was at the jugal-prefrontal contact. The postfrontal differs from that of the Newsham specimen figured as "*A. russelli*" in being less slender anteriorly, but does not differ appreciably from other specimens of *Pteroplax-Eogyrinus.* The postorbital is, as in the English specimens, a rather small element, mainly a flattened vertical plate of bone lying between the orbital margin and the squamosal; above, it broadens somewhat to a contact with the intertemporal. In characteristic embolomere fashion, it has but a small area of contact with the postfrontal along the orbital rim. The bone is little sculptured except at its dorsal margin. Although it is unfortunately far from complete, the jugal is obviously by far the most extensive of all roofing elements, occupying a broad area below the orbit and extending far forward and backward along face and cheek. Ventrally, there is a long distinct suture with the maxilla; more posteriorly, the jugal enters the lower margin of the skull. Part of the suture with the quadratojugal is missing, but most of the line of suture of jugal with postorbital and squamosal is distinct. Anteriorly, much of the area of contact with lacrimal and prefrontal is missing, and the short area of lacrimal contact shown in the figure is doubtful. There is good sculpturing on the more ventral part of the bone, but the upper portions are nearly smooth. In the "*A. russelli*" skull the orbit is essentially triangular in shape, with the jugal margin deeply concave. Here, the jugal margin is more gently curved, so that even if the prefrontal were brought more posteriorly than in Figure 3, the orbit would be much more circular in outline than in the Newsham specimen.

Both intertemporal and supratemporal are well developed, with a good sculpture pattern. The intertemporal extends forward nearly to the orbital margin, almost completely separating postfrontal and postorbital. In contrast to the tendency for reduction of the intertemporal in labyrinthodonts generally, this element is here persistently large — somewhat larger than the supratemporal. Laterally, intertemporal and supratemporal curve smoothly downward from the plane of the skull table. As preserved, the squamosal, slanting outward at about a 45° angle from the skull table, had obviously been disarticulated from the temporal elements, indicating the presence of the zone of weakness usual here in embolomeres. The tabular is well developed, with good contacts dorsally with supratemporal, parietal and postparietal, and a broad occipital contact with the last element. There was a well developed "horn," the distal part of which is missing. There is a typical slit-like otic notch lateral to the tabular.

The squamosal is a broad plate-like element, only lightly sculptured. Nearly straight contacts with the temporal elements above and the postorbital anteriorly are readily seen. Ventrally, there is a line of breakage which appears to follow the position of the sutures with the jugal and most of the quadratojugal. The position of the squamosal-quadratojugal suture near the quadrate is doubtful. As nearly as can be determined, the quadrate extends far upward toward the otic notch at the back margin of the cheek, and there is a long, nearly straight suture between quadrate and squamosal here. The posterior margin of the squamosal is not sculptured. Dorsally, the posterior boundary of the sculptured area is a well-marked and sharp ridge which descends from the anteroventral margin of the otic notch. Posterior to this ridge is a rounded channel which descends along the squamosal nearly to the articular area of the quadrate. The quadratojugal is well preserved, well developed, and well sculptured externally.

Palate (Figs. 2, 5). Most of the palate is preserved on the left side, but the pterygoid is incomplete posteriorly, the ectopterygoid is incomplete, and there are further imperfect areas. On the right, there are merely fragments of premaxilla, maxilla, vomer and palatine anteriorly; nothing remains posteriorly except a tiny pterygoid fragment.

The left premaxilla is preserved nearly completely; its rostral end overhangs the tooth row, internal to which the bone is somewhat excavated for the reception of the anterior dentary teeth.

Most of both vomers are present. The two together form a narrow internarial bar anteriorly, but broaden posteriorly. On the left a vomer-palatine suture is evident. Posteriorly, each vomer

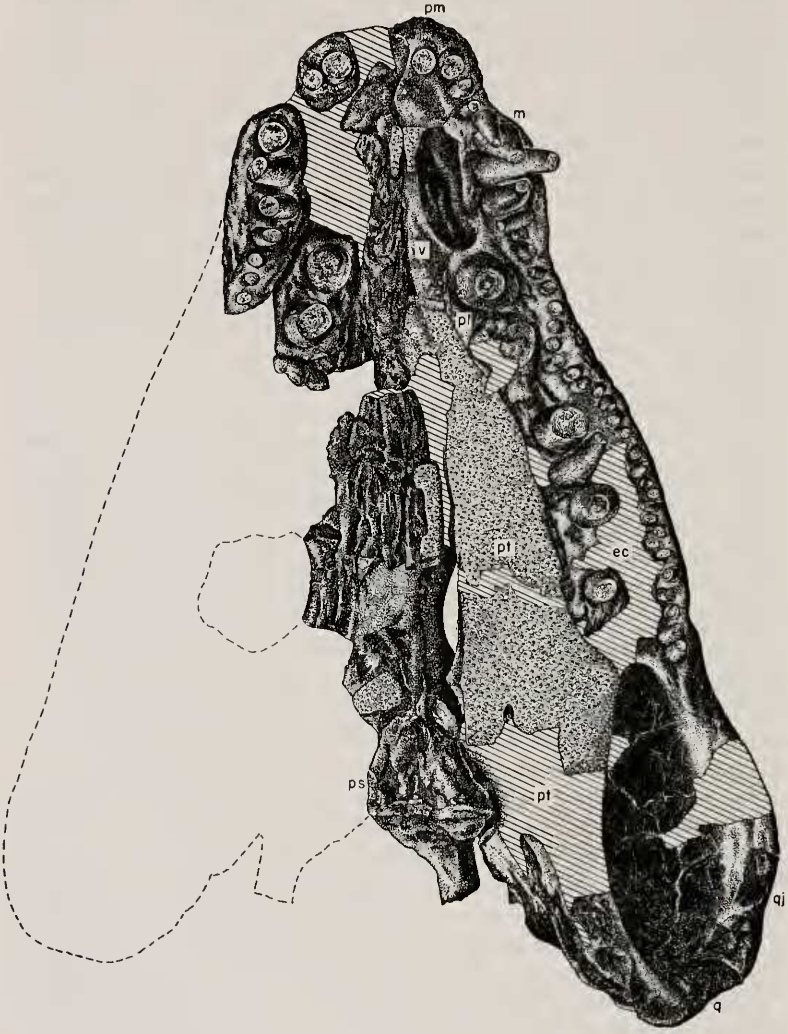

Figure 2. *Neopteroplax conemaughensis.* Palate as preserved. x⅓ approximately. Abbreviations: *ec,* ectopterygoid; *m,* maxilla; *pl,* palatine; *pm,* premaxilla; *ps,* parasphenoid covering basicranial region; *pt,* pterygoid; *q,* quadrate; *qj,* quadratojugal; *v,* vomer.

develops a ridge near its median border; the two ridges diverge toward the back, leaving as preserved a V-shaped groove between them. Posteriorly, the left vomer appears to be complete, with a truncate end in contact with the anterior terminus of the pterygoid. On both sides a shelf of bone is seen rising dorsally from the medial border of the choana toward the skull roof. Presumably this is a dorsal extension of the vomer. At their anterior ends the vomers bear a patch of shagreen teeth, and it is probable that this shagreen extended farther posteriorly in life, to continue along the pterygoid.

Almost the complete outline of the left choana is preserved, as is the medial margin of the right choana. The opening was a long oval, with the medial border somewhat concave, the lateral border convex in contour. The premaxilla entered briefly into its anterior margin, the palatine equally briefly into the posterior margin; the lateral border was formed by the maxilla, the median border by the vomer.

The maxilla, bearing the marginal dentition, has for most of its length only a very narrow exposure on the palate. It is, however, rather broader anteriorly, where it extends to the choanal margin, and appears to have broadened somewhat near the palatine-ectopterygoid suture. Posteriorly, the exact relations of the maxilla with the jugal and ectopterygoid are obscure. Most of the palatine can be seen on both sides. It is a small bone, extending little beyond the boundaries of the large tusk and replacing pit which it carries. Laterally, it is bounded by the maxilla, medially by the pterygoid, anteriorly by the vomer; posteriorly, it is in contact with the ectopterygoid, and some indication of its suture with this bone can be made out. Both palatine and ectopterygoid show some evidence of a sculpture pattern. The ectopterygoid is a long and relatively narrow element, bearing a half dozen tusks or replacing pits. Most of the medial border of the bone, with a long suture with the pterygoid, is preserved on the left side; the lateral margin and posterior end, however, are missing.

The pterygoid is the major element of the palate. Almost the entire palatal ramus is present on the left side. It bears a shagreen of small teeth as well as some indication of sculpture. The medial margin of the palatal ramus is nearly straight, indicating that, in primitive fashion, interpterygoid vacuities were, at the most, narrow slits; it is possible, however, that the vacuities extended forward to the vomerine region and that there was no contact between the two pterygoids anteriorly. The median border of each pterygoid is thin anteriorly; more posteriorly it thickens, with a double ridge facing medially. As the region of the articulation with the basipterygoid process is approached, the bone thickens further and the upper median edge curves dorsally, with the development of an articular process. Unfortunately, the actual basal articular area is missing on the left side;

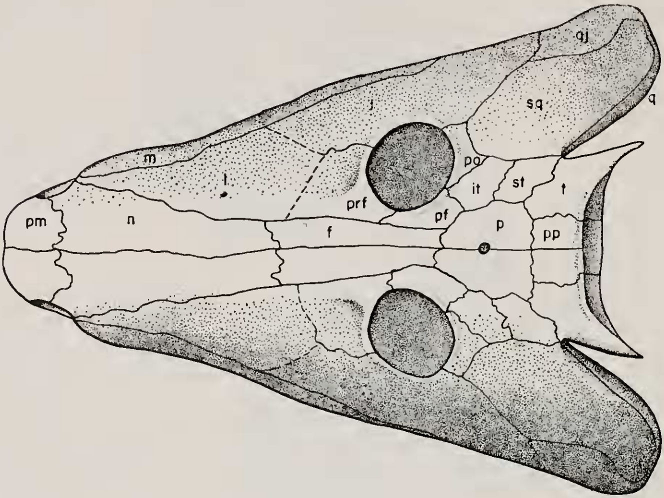

Figure 3. *Neopteroplax conemaughensis.* Dorsal view of restored skull, x¼. Abbreviations as in Figure 1.

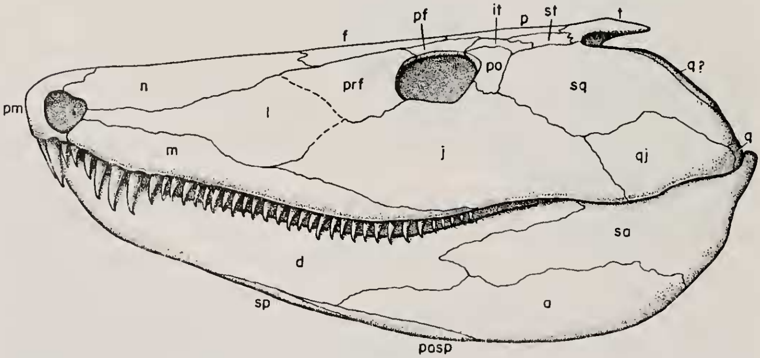

Figure 4. *Neopteroplax conemaughensis.* Restored skull and jaw in side view, x¼. Abbreviations as in Figure 1 and Plate 2.

however, a broken-off mass of the right pterygoid which includes this region is present in position close to the basipterygoid process. Narrow anteriorly, the palatal ramus gradually widens as its lateral margin passes backward along the borders of palatine and ectopterygoid. At the back end of the ectopterygoid region the lateral border, as preserved, swings outward, and then turns posteriorly and slightly medially. There was obviously no development of a pronounced lateral flange. Following a major gap, the distal part of the quadrate ramus is represented by a terminal area applied to the medial surface of the quadrate; from this, two irregular broken pieces extend forward and upward in the direction of the palatal ramus.

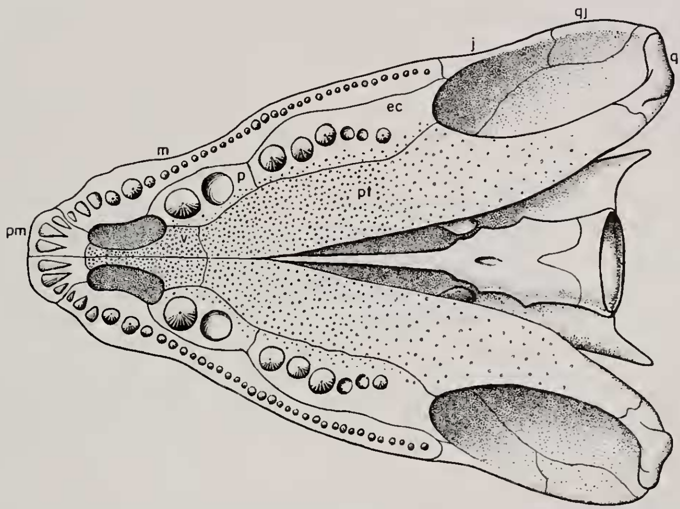

Figure 5. *Neopteroplax conemaughensis.* Restored palatal view, x¼. Abbreviations as in Figures 1 and 2.

There are no visible remains of an epipterygoid. The left quadrate is well preserved and appears to be highly developed. There is a typical articular region of the bone, bounded anteriorly by the quadratojugal and overlapped dorsally by the squamosal and posteromedially by the pterygoid. Extending upward and medially toward the otic notch between the area assigned to squamosal and pterygoid is a strip of bone which, beginning some distance above its base, develops into a long ridge (somewhat imperfect at its summit in the specimen). It is quite possible that I am mistaken as to sutures in this region, and this ridge may belong to either squamosal or pterygoid, but I gain the impression that we are dealing with a very highly developed quadrate.

Braincase. As seen from below (Fig. 2), the region of the skull where remains of the braincase are to be expected, presents a discouraging picture of broken and displaced masses and fragments of bone. In some areas the under side of the roofing bones is visible; for example, there can be seen the thickened and rounded upper margins of both orbits with, parallel to them in a more medial position, longitudinal ridges marking the lateral borders of the area occupied in life by the braincase.

Close to the posterior end is a major mass of bone, the surface of which consists of the parasphenoid expansion beneath the sphenoid region; this mass is tilted toward the left, giving a somewhat asymmetrical appearance. On either side, the broad sheet of parasphenoid curves upward about the braincase margin. The right margin of the parasphenoid is chipped and imperfect here; a concavity on the left side near the back may be likewise an imperfection, but may possibly be part of the lower margin of the fenestra ovalis. The posterior end of the parasphenoid is missing; at the back, as preserved, a median groove represents the beginning of the separation between the two basitemporal processes. The basioccipital and exoccipitals are broken off, so that little can be said of the crushed occipital region, and nothing of the condyle (presumably single). The lateral braincase walls in otic and sphenoid regions are very poorly preserved.[1] The left basipterygoid process is present, although incomplete at its tip; the right is presumably present but concealed by the articular process of the pterygoid. The base of the process is partly defined by a characteristic groove for the carotid artery. Between and slightly to the rear of the basipterygoid processes there is an oat-shaped pit in the mid-line of the parasphenoid; this is bounded on either side by a low ridge. There is no indication of a foramen within this pit; possibly it is a remnant of the embryonic hypophysial pocket.

The parasphenoid rostrum, rounded ventrally, is preserved for 15 mm. forward from the basipterygoid processes. Following a gap, another section of the parasphenoid, some 4 cm. long, is

[1] I may incidentally note that in the *Eogyrinus* braincase, figured by Watson (1926, fig. 18), the exoccipital appears to be missing and the supposed vagus foramen (X) is presumably the fenestra ovalis (cf. his fig. 12, *Palaeogyrinus*, in which the small exoccipital is present).

present, its ventral surface turned toward the left side of the skull. This section is tipped by thin fragments of shagreen-covered bone. It is tempting to think of this as indicating a shagreen surface on the parasphenoidal rostrum. More probably, however, the association is fortuitous, and this material is presumably a displaced fragment of the right pterygoid. Without apparent break from the parasphenoid there extends upward from the (morphologically) right side of this fragment a sheet of bone, apparently reaching the skull roof, which presumably represents part of the sphenethmoid. More anteriorly, there are no readily interpretable remains of parasphenoid or sphenethmoid.

Lower jaw (Pl. 2; Fig. 6). The right lower jaw is nearly complete. As preserved, its length is 332 mm.; about 1 cm. of the tip is missing, giving a length in life of approximately 342 mm. Except for this missing tip and a chipping-off of the sculptured surface of the dentary over a fraction of the area above the splenial, the outer surface is well preserved. The general jaw shape is that of a typical embolomere, with one notable exception.

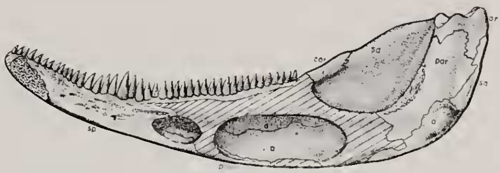

Figure 6. *Neopteroplax conemaughensis.* Jaw in internal view; restored areas hatched. Abbreviations: *a*, angular; *ar*, articular; *cor*, coronoid; *d*, dentary; *par*, prearticular; *posp*, postsplenial; *sa*, surangular; *sp*, splenial, x1/5 approximately.

In such forms as *Pteroplax* and *Archeria*, there is a major unsculptured dorsal expansion of the surangular which rises, with an outward roll, well above the general line of the dorsal margin of the jaw. This expansion is almost totally lacking in the present specimen, the contour of the upper margin of the surangular being only gently convex. In consequence, the jaw lacks the unusual depth in the "angular" region seen in seemingly more typical embolomeres. The nature of the sculptured pattern of the external surface may be seen in Plate 2. Close to the lower margin of the jaw in the splenial region there is a well-marked groove for the lateral line canal; this fades out posteriorly, however, and in contrast to *Archeria* cannot be traced backward and upward over the surface of the angular.

Except for a diagrammatic representation in Watson's restoration of the "*Eogyrinus*" skeleton (Watson 1926, fig. 28) no attempt has ever been made to trace the sutural pattern of the outer surface of an embolomere jaw, and I find the task here a difficult one. For the most part, the sutures bounding splenial and postsplenial can be fairly readily determined and these elements have a typical labyrinthodont development. As figured, they appear to be much narrower than is actually the case, due to the fact that the outer surface of the jaw ramus curves strongly medially toward its lower margin, and the two elements are hence much fore-shortened in the illustration. Posteriorly, the suture between surangular and angular can be seen running forward from the posterior rim of the jaw somewhat below its half-height and, more dorsally and anteriorly, the suture between surangular and the dentary, which overlaps it externally back of the termination of the tooth row, is readily determined. Farther forward, however, the sutural boundaries of these three elements are far from certain. In most labyrinthodonts the surangular tapers rapidly forward below the dentary; here it appears to extend forward for a considerable distance.

The articular is a massive wedge-shaped element, sheathed medially by the prearticular, and posteriorly and externally by the surangular; anteriorly, it descends into the adductor fossa, but this area is not well seen in the specimen. There is no retroarticular process. The concave articular surface lies essentially in a horizontal plane; it is saddle shaped, concave throughout in anteroposterior section, convex in transverse section, its central portion higher than either extremity. Mediolaterally the articular surface traces an arc of about 45°. Its outer end, which projects well out beyond the plane of the surangular, lies at right angles to the long axis of the jaw, its inner end curves well forward. The articular surface is bounded the length of its posterior margin by a high ridge (somewhat imperfect in the specimen) which is thin and sharp-crested medially, thicker and blunt-tipped laterally. The anterior border is for the most part lower, but there is a prominent ridge for a short distance above the adductor fossa. The articular region is in general quite similar to that of *Pteroplax*.

In internal view the inner surface of the surangular is well exposed posterodorsally. As in other embolomeres, the upper margin of the surangular rolls smoothly outward but, as mentioned above, the high flange developed in this region in *Pteroplax* and *Archeria* is not present here. The posterior end of the coronoid series is seen covering the medial surface of the dorsal edge of the surangular posterior to the tooth row and projecting slightly above the general dorsal contour of the jaw. Farther forward the inner surface of the external sheathing bones of the jaw is sufficiently exposed to show much of the presumed surangular-angular suture and of the dorsal boundaries of postsplenial and splenial.

At the inner end of the articular area a broad sheet of bone descends along the posterior margin of the inner surface of the jaw and forms part of the low inner boundary of the adductor fossa. Most of this bony sheet is formed by the prearticular. Roughly parallel to the curved dorsoanterior margin of this bony sheet is a line of rugosities which not improbably marks the ventral limit of the area of insertion of a medial sheet of adductor musculature. A similar but much more sharply marked area is to be seen in *Archeria* and, apparently, *Pteroplax*. The back edge of the jaw in much of this region is a sharp crest. The surangular here is not confined to the outer surface, but is exposed as well over a narrow strip of the inner surface of the jaw adjacent to the prearticular. The angular is also exposed on the inner surface ventral to the prearticular. It covers a much broader area here than the surangular and bears posteriorly and ventrally a very prominent tuberosity which would appear to be present but less developed in *Pteroplax* and *Archeria*. Presumably this is associated with musculature — possibly a depressor of some type.

The diagnostic feature of the embolomere jaw is the presence on the inner surface of two large meckelian fenestrae. In the present specimen the bars separating these fenestrae from one another and from the adductor fossa have been destroyed, and the surface of much of the coronoid and prearticular regions above the fenestrae is absent. The portions of the inner surface remaining are, however, sufficient to mark out the roots of the bars bounding the fenestrae and thus to indicate the original presence of the embolomere pattern, as restored in Figure 6. A chip of the lower margin of the jaw is missing at the point where there should be present the anterior end of the bar between adductor and posterior meckelian fossa, but the preserved lower edge of the bone (formed by the angular) is thickened in a fashion expected at the base of this bar. Farther forward the lower rim is again imperfect at the posterior end of the splenial, but thickenings here show definitely the anterior and posterior boundaries of the bar between the two meckelian fenestrae. Although most of the coronoid region is gone, a small fraction preserved midway of the tooth row shows a shagreen of small teeth comparable to those which extended most of the length of the coronoid series in *Pteroplax* and which presumably existed here.

From the anterior end of the anterior meckelian fenestra to a point not far back of the symphysis, the inner surface of the jaw is well preserved. Dorsally, there is an essentially horizontal shelf, non-denticulated, extending inward about 1 cm. from the tooth row. At the inner edge of this shelf there is a strong anteroposterior ridge with a smoothly rounded surface. Below this ridge the inner surface descends to the lower margin in an essentially vertical plane, but is somewhat concave in transverse section. This area is similar in pattern in both *Pteroplax-Eogyrinus* and *Archeria*. Presumably, much of the inner surface is occupied by the splenial, and it is probable that the anterior ends of the prearticular and coronoid series enter into the composition of the dorsoposterior part of this area. I have not, however, been able to determine sutures here with certainty.

Dentition. In no instance is a complete tooth present; although there is definite evidence of almost every tooth position, the teeth are generally represented only by broken stumps or alveoli. The tooth bases are all essentially subcircular in outline. Little can be said as to tooth shape — whether, for example, they were recurved at their tips or whether compressed or not (since in general the basal parts of teeth whose shafts are compressed are nevertheless circular in section). Nor are the data sufficient for comment on the nature of tooth replacement. This was presumably of the alternating type common in early tetrapods, but nearly all marginal teeth were present in this specimen at death.

The marginal tooth row in the upper jaw included about 40 teeth. There were three premaxillary teeth, the first two large, with basal diameters close to 10 mm., and slanting somewhat backwardly, the third small. The first maxillary tooth is small; beyond this, however, there develops a "canine" region, as in various other labyrinthodonts. There is no one specific canine or canine-replacement pair but, rather, a series of four or five teeth, all of which are enlarged to a variable degree, with a maximum basal diameter of about 15 mm. Back of this region there follows a row of about 30 teeth of small size, averaging 5.5 to 6 mm. in basal diameter. As seen in Figure 2, the "post-canine" tooth row as preserved does not form a straight linear series, for there is an inward curvature opposite the palatine-ectopterygoid suture; this, however, is due to breaks in the maxilla and consequent displacement. In the lower jaw, as in the upper, about 40 marginal teeth are present. As far as can be determined, the teeth are nearly uniform in size, although there appears to be some slight increase over the mean at a point about one-third the way back along the tooth row.

On the palate, a shagreen of small denticles covers the portions of the vomers on which the surface is well preserved and extends the length of the expanded palatal ramus of the pterygoid. As in other known embolomeres, vomerine tusks are absent. The palatine bears an enormous tusk-pair, with a basal diameter of the fully developed left tooth of about 25 mm.; as is frequently found to be the case, each palatine bore one functional tusk at the time of death, the second being represented by a large replacement alveolus. A row of tusks was present on the ectopterygoid, much as in *Pteroplax*. On the preserved side there are six tusks or alveoli, decreasing in size posteriorly; the first of the series has a basal diameter of about 18 mm., the last 13 mm.

The anterior end of the lower jaw is too imperfect to tell whether or not symphysial teeth were present internal to the marginal row. Posteriorly, a denticulated area of the coronoid series is preserved, but the anterior extent of this denticulation is uncertain and denticles are not present toward the anterior end of the jaw.

Nomenclature. In the present skull we have for the first time clear and positive evidence of the presence in North American Pennsylvanian of large embolomeres of the general *Pteroplax-Eogyrinus* type which were apparently common in the Upper Carboniferous of Great Britain and are best known from the splendid Newsham materials (Hancock and Atthey 1869, 1870, 1871, Atthey 1877, Watson 1926). Prof. Watson distinguished two genera at Newsham, *Pteroplax* and *Eogyrinus,* on the basis of the nature of the tabular "horns."[1] Dr. Panchen informs me that although the features on which Watson originally differentiated the two genera may not be valid, the two may, nevertheless, be distinguished on other grounds. But whether distinct

[1] The original describers did not designate holotypes. It seems proper, however, that the skull table figured by Hancock and Atthey in plate XV, figure 1, 1868, and by Atthey in plate XII, 1877, be designated as the holotype of *Pteroplax cornuta,* and the skull described and figured by Atthey in 1876 as a specimen of "*Anthracosaurus russelli*" is herewith designated as the type of *Eogyrinus attheyi* (Watson's number D.M.S.W. 27).

or not, the *Pteroplax-Eogyrinus* materials together present a picture of a large, massively built embolomere with a moderately long snout, which was obviously a piscivorous, aquatic inhabitant of the Coal-Measures swamps. The present form was obviously similar in structure, as far as known, to these British amphibians, and was presumably comparable in habits.

But while close to *Pteroplax-Eogyrinus,* the present form is definitely distinct. Certain differences in details of sculpture and sutural pattern might be regarded as individual variations or, at the most, specific in nature, and the apparent contrast in orbital shape is not important. There is, however, a notable difference in the lower jaw, as noted earlier. In all known material from Newsham the jaw is excessively deepened posteriorly, due to a conspicuous outrolled dorsal development of the surangular which is absent in the present specimen. This departure from the typical embolomere jaw structure is definitely a point of at least generic rather than specific distinction. *Pholiderpeton* is a further European type with which comparison might be made. This is inadequately known. In general, there is no clear distinction, as far as the material has been described, between *Pholiderpeton* and members of the *Pteroplax-Eogyrinus* series. Possibly *Pholiderpeton,* like our specimen, lacked the rolled-out surangular. But the condition is unknown in the type specimen, and the jaw material of a second specimen which Watson ascribed to this genus is imperfect in this region.[1]

No name already applied to an American Carboniferous amphibian seems definitely applicable to the present form. In consequence, this skull is herewith made the holotype of a new genus and species of embolomere as *Neopteroplax conemaughensis,* with the combined generic and specific characters being (apart from size) the absence of the expanded dorsal flange of the surangular, the relatively numerous and relatively small marginal teeth, a more circular orbital shape than in *Pteroplax* and the absence of the anterior coronoid tooth development seen in *Eobaphetes.*

[1] I wish to thank Dr. R. M. C. Eager for examining the part of this second specimen contained in the Manchester Museum collections.

II. Other Large American Carboniferous Embolomeres

Discovery of new and restudy of old materials is gradually increasing the number of known remains of American Carboniferous embolomeres. In general, they appear to sort out into two size groups, the larger of about the proportions appropriate to the skull just described, the smaller of about the size of typical Texas *Archeria* specimens or the type material of *Cricotus* from Illinois. It is quite possible that certain of the smaller specimens may be growth stages of larger animals. I do not, however, believe that this is generally the case. Growth stages of Paleozoic amphibians, including larval stages, may, of course, be recovered under such favorable conditions as, for example, the famous Linton cannel. But experience with large quantities of Permian labyrinthodont materials strongly suggests that post-larval growth was very rapid until essentially ''adult'' size was reached, after which further increase in size was very slow indeed. For example, in large amounts of material of *Eryops* and *Trimerorhachis* collected in non-selective fashion, few specimens from any given formation show any marked deviation from the ''adult'' norm. One may thus reasonably regard the larger and smaller Carboniferous embolomere specimens as representatives of two series with, presumably, differing types of food habits and ecological adaptations. We will here note other known representatives of the series of larger forms, and leave discussion of smaller Carboniferous embolomeres to a later occasion. The finds are here listed in essentially stratigraphic order, beginning with the oldest.

Canso group, Nova Scotia. I have (1958) described, as *Pholiderpeton? bretonense,* the greater part of a lower jaw, seen from the outer surface, from the Point Edward formation, Canso group, of Cape Breton. The sculpture and contours suggest that we are dealing with an embolomere, although, unfortunately, the diagnostic features of the inner surface are not ascertainable.

Figure 7. Sketch of labyrinthodont jaw from the Point Edward formation, from the collections of the Canadian Geological Survey. x½.

Dr. Wann Langston has since discovered in the collections of the Canadian Geological Survey a labyrinthodont jaw (no. P-1503/10015) collected at Point Edward by Dr. W. A. Bell in 1915, which he has kindly forwarded to me for study, and of which a sketch is given in Figure 7. The jaw is nearly complete, lacking only the symphysial region. The surface, however, is imperfect. As can be seen, the specimen is but about two-thirds the size of the *P.? bretonense* type. The contours of the present specimen and the type are identical as far as the latter is preserved,[1] and, as suspected in the case of the type, the outlines are those characteristic of anthracosaurians in general and embolomeres in particular, in the deep angular region and well-expanded dorsal flare of the surangular. As in the type, the teeth are slender and closely spaced. It is unfortunate that the inner surface cannot be seen and hence here, as in the type, it is impossible to say whether or not diagnostic embolomere features were present. This jaw appears to represent a growth stage of *P.? bretonense* or a closely related form.

Dr. Donald Baird has collected further labyrinthodont materials from this formation at Point Edward. In addition to a skull fragment of the loxommid *Spathicephalus,* the materials include (Princeton University no. 17190) a clavicle, a small phalanx, 10 mm. in length, and a single ventral scale, 14 mm. long. The clavicle (Fig. 8) has a long stem extending upward and outward at about a 60° angle. This clavicle is appropriate for an anthracosaurian, rather than a presumably flatter-bodied loxommid. As may be seen from the figure, there is a characteristic triangularly-expanded ventral plate, measuring 8 cm. along its medial border, which is about 5 cm. from the base of the tapering, slender "acromial" process.

The reference of the Point Edward labyrinthodont jaw to *Pholiderpeton* was for convenience only; this English genus appeared to be of approximately the same age. Recently, however, Panchen and Walker (1961) have shown that the ages of various British deposits, including those in which *Pholiderpeton* was reported, are not as great as once thought. On the other hand, "*Pholiderpeton*" *bretonense* may be older than previously stated. The Canso group, to which the Point Edward formation pertains, has been regarded as equivalent to about the middle of the European Namurian and very early Pennsylvanian (Moore *et al.* 1944) or very late Mississippian (Weller *et al.* 1948).

[1] Superposition suggests that my original estimate of the jaw length of the type was too high, and that this figure may have been but about 30 cm.

Studies now in progress by Mr. Edward S. Belt of Yale University suggest that, in agreement with the work of Bell (1944) and Copeland (1957), the Point Edward beds are at least as early as Namurian A or possibly late Viséan.

Morrow series, Arkansas. Half a century ago Moodie described a fragment of labyrinthodont skull and an embolomere jaw as *Eobaphetes* [*Erpetosuchus*] *kansensis* (Moodie 1911; 1916, pp. 189-192, fig. 42).[1] These specimens came, in all probability, from the Baldwin coal of the Woolsey member of the Bloyd formation of the Morrow series in Washington County, Arkansas,[2] and

Figure 8. A clavicle, perhaps pertaining to *Pholiderpeton? bretonense*, from the Point Edward formation. x½.

[1] The 1911 figure of the jaw is approximately ×1/3; his 1916 figure, said to be ×1/3 is approximately ×28/100.

[2] The locality and horizon from which this material is derived has long been a source of perplexity to students of early tetrapods. Preserved in slabs of impure coal, they were stated by Moodie to have come from "the Coal Measures of Washington County Kansas," and are so entered in the records of the U.S. National Museum. But the sediments of Washington County Kansas are of Cretaceous and Permian age and contain no "Coal Measures." Through the courtesy of Drs. Nicholas Hotton, III and G. A. Cooper of the U. S. National Museum, the history of the specimens has been traced. It was part of a collection assembled by Prof. Gustave Hambach of St. Louis which was purchased by that Museum in 1909. It mainly consisted of fossil echinoderms, but also included a few other animal and plant fossils which Professor Hambach had picked up in the course of his search for echinoderm materials. As far as known, he never visited Washington County, Kansas, but did work in Washington County, Arkansas and, in fact, described echinoderms of the genus *Pentremites* from the Brentwood limestone in that county (Hambach 1903). Immediately above this limestone is the Baldwin coal. This coal was actively worked at the time at which Hambach's field work was done. It seems certain that this labyrinthodont material was collected during the course of his Arkansas field work, and the substitution of "Kansas" for "Arkansas" is surely due to misreading of the original labels.

hence from a horizon very early in the Pennsylvanian, close to the Namurian-Westphalian boundary of the European classification and equivalent to a low position in the Pottsville series of the eastern interior coalfield of the United States. The jaw is of especial interest as the geologically oldest specimen in which the typical embolomere construction of the inner surface of the jaw is known. Of further interest is the fact that current work by James H. Quinn indicates that the Hale formation underlying the Bloyd without, as far as known, any marked gap, is equivalent in age to the E_2 zone of the European early Namurian. *Eobaphetes* is thus far older than the skull from Swanwick, which Panchen and Walker (1961) cited as the oldest anthracosaurian then known; this English locality is in the Communis zone of late Westphalian A.

The animal represented by the jaw was of large size, although somewhat smaller than *Neopteroplax.* The structure is typically embolomerous, but there are two definite points of difference from *Neopteroplax.* (1) As shown in Moodie's figures, the anterior part of the coronoid region is well supplied with small teeth, whereas this region is bare in *Neopteroplax.* (2) The lower jaw teeth are much stouter than in *Neopteroplax* and, in correlation, fewer in number; on the average, the tooth diameter at the base is about 7 mm., as compared with 5 mm. in *Neopteroplax*, and the total number of dentary teeth may be computed as about 30, as compared with a considerably higher count in *Neopteroplax.* There is no guarantee that the skull fragment (designated by Moodie as the holotype) is part of the same individual as the jaw. From Moodie's figure, one gains the impression that we are dealing with an animal of different character, with smaller and more closely crowded teeth. However, Dr. Nicholas Hotton, III has checked the specimen for me, and reports that Moodie's figure is inaccurate, and that the upper jaw dentition, as regards size and spacing of the teeth, is closely comparable to that of the lower jaw.

The "ruggedness" of the dentition, with relatively stout individual teeth and a relatively low tooth count, shows that we are dealing with a form quite distinct from *Neopteroplax* and from various small embolomeres (as *Leptophractus, Archeria*) with numerous slender teeth. The dentition is comparable to that of the form discussed below as *Anthracosaurus lancifer* from Linton, Ohio; but in view of the considerable stratigraphic interval concerned, and the seemingly distinctive nature of the coronoid and symphysial dentitions, *Eobaphetes kansensis* and the Linton form may be regarded as generically distinct. The generic name chosen by Moodie is, of course, unfortunate, since this embolomere has no close relationship to the loxommid *Baphetes*.[1]

Riversdale group, Nova Scotia. Centra of a large embolomere, with a maximum height of 35 mm., were collected by William F. Take of the Nova Scotia Museum of Science, Halifax, on the shore of a cove northeast of Cape Linzee, Inverness Co., Nova Scotia, in 1959. They were found in a sandstone some distance above the Ten Inch Coal Seam of the Port Hood formation of the Riversdale group, equivalent to Westphalian A of Europe, and the lower part of the Pottsville series of the Appalachian region.

Cumberland group, Nova Scotia. Sediments of this group, believed to be essentially equivalent to Westphalian B, are best known from the Joggins cliff exposures of Nova Scotia, famous for the small tetrapods discovered there in erect trees. A few finds from this section may pertain to large embolomeres.

Marsh in 1862 described as *Eosaurus acadianus* two very large disc-shaped objects, presumably central structures of some sort, said to have come from a layer near the top of division 4 of the Logan-Fletcher section of the Joggins exposure, rather high in the Joggins formation of Bell (1914). These discs, with diameters of about 50 mm., do not show any of the distinctive features generally seen in embolomere central elements. But if from the Carboniferous, there is no other group to which they can well be assigned, for we know of no huge sarcopterygian of this age, nor would such a form, if present, be liable to have such well-ossified centra. If belonging to an embolomere, the usual exponential relations between vertebral diameters and linear dimensions would indicate a giant form. Marsh notes the similarity of these centra to those of ichthyosaurs. It may be suggested that there has been confusion as to the pertinence of this specimen, and that these bones are actually centra of a Liassic ichthyosaur.

"*Baphetes*" *minor* was described by Dawson (1870; 1894, p. 268; Moodie 1916, p. 187) from an impression in sandstone of

[1] Search in the National Museum collections has resulted in the finding of a slab containing additional materials of this specimen. Its development and study will add to our knowledge of the *Eobaphetes* skull and jaw.

an incomplete dentary (Fig. 9) found in the Joggins bluff between Ragged Reef and the Joggins coal mine. The holotype (never before figured) is MCZ 1053. The specimen is about 15 cm. long; it shows impressions of much of the middle and

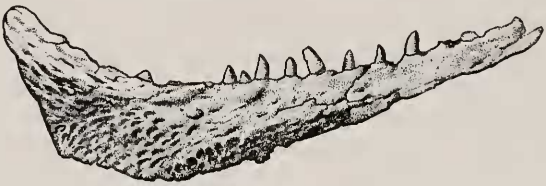

Figure 9. The type of *''Baphetes'' minor,* drawn from a cast of the original impression. x½.

posterior portions of the outer side of a right dentary, and a number of teeth are present as well as impressions of others. For most of the preserved length of the tooth row alternate labyrinthine teeth were present, with intervening alveoli. There is no positive evidence as to what group of labyrinthodonts this jaw pertains. The upward curvature of the jaw margin, posteriorly, is somewhat suggestive of an embolomere rather than a rhachitome, but, on the other hand, the sculpture is stronger than is usual on an embolomere dentary. The contours of the bone suggest an animal rather smaller than *Neopteroplax* — say about three-fourths of the size of the skull described above. This impression is heightened by the fact that the teeth (including alveoli) are spaced about 45 mm. apart, as contrasted with a higher figure in *Neopteroplax.* There is, of course, no evidence as to whether this form has anything to do with the loxommid *Baphetes.* The exact locality of the find is unknown, but it was

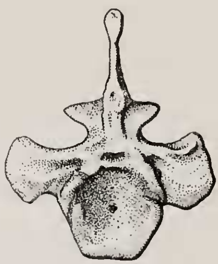

Figure 10. End view of an embolomerous centrum and neural arch from the Joggins, Nova Scotia. x½.

presumably in division 3 of the Logan-Fletcher section (1908), and hence higher in the section than *Eosaurus* and near the top of the Joggins formation.

Finds made at the Joggins by a 1956 expedition from this museum were few in number, but include an embolomere dorsal vertebra, MCZ 3220 (Fig. 10), with a width in the central region of 29 mm. — a size appropriate for such a form as "*Baphetes*" *minor*. No intercentrum is present; neural arch and centrum are fused, indicating "adult" conditions. This vertebra was collected from the Forty Brine Coal Seam, one mile north of the Joggins pier, and hence in the lower part of Division IV of the classic section.

Stellarton group, Nova Scotia. From the Albion Mine at Stellarton, Nova Scotia, there was collected more than a century ago a pelvis, described by Watson (1926, fig. 27), which is comparable to those of embolomeres. The dimensions are nearly double those of typical *Archeria* pelves and hence appropriate for an embolomere of large size. The pubis is much shorter than in *Archeria*. The embolomere type of pelvis is very probably of a very primitive nature (that of *Ichthyostega* is basically similar) and there is, of course, no absolute guarantee that the animal which owned this pelvis was actually an embolomere. But, on the other hand, there is no positive reason to believe that the pelvis pertains to the loxommid *Baphetes,* the type of which is also from the Albion Mine. The horizon is the basal, Albion member of the upper division (Division II) of the Stellarton Group of Bell's classification (1940), which he regards as lying approximately at the base of Westphalian C. The horizon thus appears to be definitely later than those of the Joggins finds, but equally definitely earlier than that of the famous Linton deposit at the summit of the Allegheny series.

Allegheny series of Linton, Ohio. As noted earlier, I had at one time (1930) assigned to the Embolomeri a considerable amount of material from the famous Linton cannels, under the then prevalent assumption that all Carboniferous labyrinthodonts were embolomeres. In later years, however, it has become apparent that this is far from being the case (Romer 1947, p. 69, etc.), and careful study of the Linton material by Dr. Donald Baird indicates that only a restricted number of specimens from this locality can be reasonably interpreted as embolomeres. Certain of these, including the types of *Leptophractus obsoletus* and *Ichthyacanthus platypus* Cope are animals of small size, and the slender and closely crowded teeth of the *Leptophractus obsoletus* type (as developed by Dr. Baird) suggest that this is not to be regarded as a growth stage of the larger form described below.[1]

Of a large Linton embolomere, the best preserved specimen is American Museum of Natural History specimen 6830, of which obverse and smaller reverse are figured by Cope (1875). The obverse, as seen in his plate XXXVIII, figure 2, shows the left surface of the muzzle of a large amphibian with, below it, the upper margin of much of a lower jaw.[2] The sculpturing of the muzzle is none too well preserved. An oval depression near the left of his figure is obviously the left external naris. A groove below it can be reasonably interpreted as lying along the premaxillary-maxillary suture. Not seen on the figure but apparent on the specimen was a low rugose ridge running backward from a point below the middle of the posterior margin of the naris.

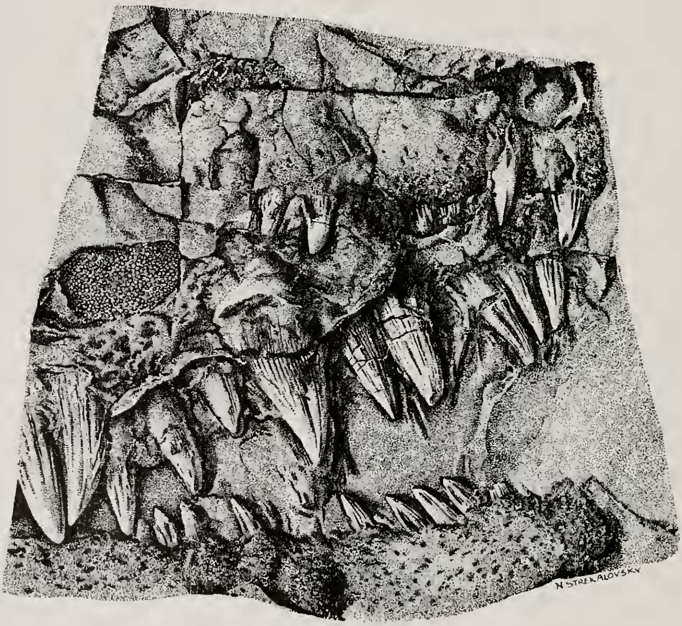

Figure 11. *Anthracosaurus lancifer.* Cast from mold after etching, of specimen figured by Cope (1875), plate XXXVIII, figure 2.

1 Cope's figure of the type (1875, pl. XXXIX, fig. 1) is stated to be two-thirds natural size. It is actually natural size.

2 Cope's figure is said to be four-sevenths natural size. The reduction is actually three-fourths.

The line of this ridge, somewhat arched dorsally, can be traced backward for most of the length of the block; during etching of the block, a sawtooth suture became evident here, and a second suture could be traced a short distance backward from the naris farther dorsally. There, two sutures lie in the position of the maxillo-lacrimal and lacrimo-nasal sutures of *Neopteroplax*.

After etching by Dr. Baird, this slab (Fig. 11) shows the imprint of a comparable region of the right side of the muzzle. The right naris, close to the right edge of the block, is well outlined. A considerable portion of the maxillary, with a lightly pitted sculpture, is present below and back of the naris. Above this area two breaks are present running backward from the narial margin and diverging posteriorly. These breaks lie at the positions at which the maxillo-lacrimal and lacrimo-nasal sutures were seen on the other side, and have obviously occurred along the suture lines.

The etched surface shows clearly the inner margin of the tooth-bearing rim of the left maxilla, and a portion of the left side of the palate, from the anterior portion of the ectopalatine region forward past the tusk-and-pit-bearing palatine element to the region of the left choana; a well-marked anteroposterior ridge represents the external border of this opening. At the left there is seen a detached area of finely denticulated bone, presumably a fragment of pterygoid.

It was not clear from the specimen as figured by Cope whether the lower jaw seen was the right or left. The mold (Fig. 11)

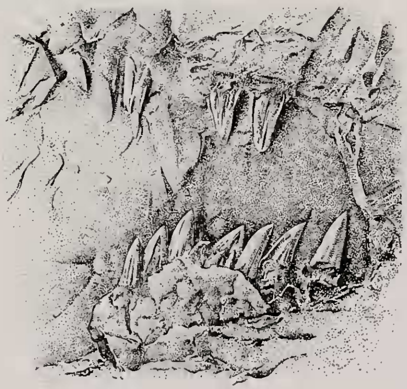

Figure 12. Cast from the mold of a small reverse slab of the specimen shown in Figure 11, illustrated before etching in Cope's 1875 plate XXXVIII, figure 1.

shows that it is the right jaw ramus, of which the upper margin is present for most of the length of the dentary. The external surface of the dentary has a lightly pitted surface. Etching of the reverse specimen (Fig. 12) shows the presence of a highly rugose area anteriorly; this is obviously the symphysial area, indicating that the anterior end of the ramus is essentially complete.

A fairly comprehensive knowledge of the dentition can be obtained from this specimen (Fig. 13). In the upper jaw, the dentition of the right side is not too well preserved, and we merely gain a general picture of a series of marginal teeth toward the front of the mouth which are broad based (an effect partially

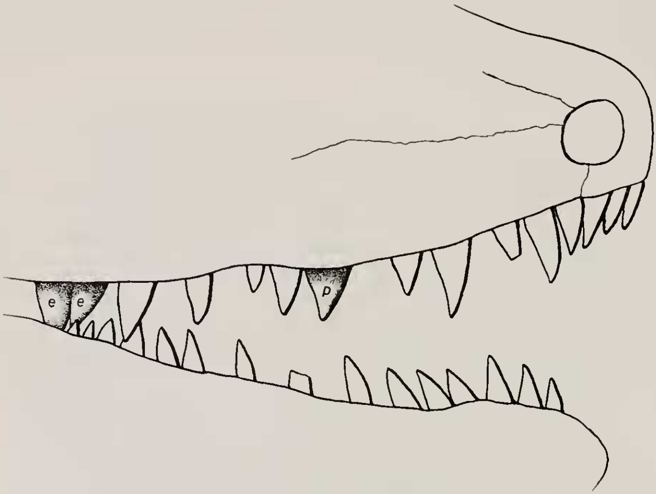

Figure 13. Diagrammatic restoration of the "muzzle" and jaw margins of *Anthracosaurus lancifer*, based on American Museum of Natural History specimen 6830; composite from the two sides of the specimen. Only teeth actually present are indicated. In addition to the marginal tooth row, the palatine (*p*) and anterior ectopterygoidal tusks (*e*) are visible. x½.

but not entirely due to crushing), slightly recurved at their tips, and striated for most of their length. The teeth extend about 15-17 mm. beyond the edge of the maxilla, and measure 8-10 mm. in diameter at the outer rim of the maxilla. The left maxillary tooth row is seen to better advantage from the inner side. Here the teeth are visible for their full length. At their bases they are essentially stout cylinders, the tapering which gives them a blunt appearance taking place beyond the point where they emerge from the rim of the maxilla. There is some development of a "canine" region, tooth length reaching a peak at the fifth maxillary tooth. The tip of this tooth is broken off, but its length in life was on the order of 35 mm. and its basal diameter is 13 mm. Back of this point there is some reduction in tooth size. The posterior maxillary teeth are imperfectly preserved, but those lying opposite the posterior part of the palatine and anterior part of the ectopterygoid would appear to have average lengths of about 25 mm. and basal diameters of 8-10 mm.

Much of the lower jaw dentition is seen in Figures 11 and 12 and Cope's plate XXXVIII (1875). The teeth are more uniform in size than in the upper jaw, and relatively short, none extending more than about 12-13 mm. above the outer rim of the dentary, with (as seen in Figure 12) about 6-8 mm. of their bases concealed within this rim. In Figure 12 are seen three well developed anterior teeth not well shown in Figure 11, and, internally placed, three much smaller teeth. It seems probable that the latter are symphysial dentary teeth, not described, to my knowledge, in other embolomeres, but known in certain other labyrinthodonts. Back of the symphysis the inner surface of the jaw is not preserved, and hence it cannot be told whether or not the anterior part of the coronoid series was denticulate, as in *Eobaphetes kansensis*, described above.

Assuming that the posterior extent of the marginal tooth row was similar to that found in other embolomeres, one can make a close estimate of numbers of marginal teeth. Of maxillary teeth and presumed alveoli, 14 are present to a point opposite the first ectopterygoid fang. Beyond this, to the assumed end of a "normal" tooth row, there is room for about 11 additional teeth. Premaxillary teeth are incompletely preserved, but two can be seen on the left side in Cope's figure and a third, not seen in the figures, was present on the front edge of the slab. This gives a total number of upper jaw teeth of about 28 — a figure markedly lower than in such a form as *Neopteroplax*, for example, but a bit higher than that of *Anthracosaurus russelli* as described by Watson (1929). In the lower jaw, 16 teeth or assumed alveoli can be counted in front of the position of the first ectopterygoid tusk. Presumably the tooth row continued, as in the upper jaw, for a further distance to accommodate about 11 additional teeth, giving a total of about 27 dentary teeth — again, a low figure for an embolomere, but close to that present in the Arkansas jaw.

As expected in a presumed embolomere, there is no indication of vomerine tusks, but tusks are well developed on palatine and ectopterygoid. The palatine tusk (accompanied by a pit for its replacing "twin") is a very large tooth, 45 mm. in length and 25 mm. in basal diameter. On the ectopterygoid, following a considerable gap, are two tusks of more modest size, the one completely preserved being about 37 mm. long and 17 mm. in diameter at the base. Presumably there were further ectopterygoid tusks behind the two preserved. Both palatine and ectopterygoid tusks are well striated for most of their lengths, but smooth at the tips.

Rather surely this specimen is an embolomere. This is strongly suggested by the absence of vomerine tusks, and suggested to a lesser degree by the lightness of the sculpture pattern. Still further indication is the fact that, as preserved, the skull was crushed from side to side rather than dorsoventrally as is common in flatter-headed temnospondyls. The size was considerable. We have a reasonably accurate measurement of skull length from snout to anterior ectopterygoid tusks. If the proportions were as in *Neopteroplax*, for example, the skull length to occiput would

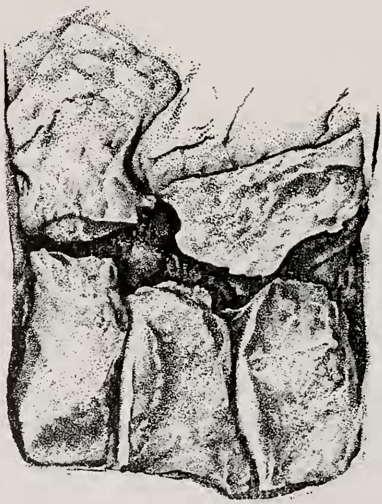

Figure 14. Embolomerous vertebral elements from Linton. From etched reverse of specimen shown in Cope's (1875) plate XXXIX, figure 3. Natural size.

have been approximately 355 mm., i.e., somewhat greater than that of *Neopteroplax*. The jaw length would have been about the same, giving, again, a figure in excess of that of *Neopteroplax* and one rather considerably in excess of the measurements of the Arkansas jaw and the Nova Scotia *"Pholiderpeton."*

Apart from large isolated scales of presumed embolomere type, two further Linton specimens may well pertain to this animal. One is a small block (American Museum of Natural History 6969) the counterpart of which (since lost) Cope figured (1875, pl. XXXIX, fig. 3) as showing vertebral centra. This specimen, as developed by Dr. Baird (Fig. 14), shows two centra and an intervening intercentrum of embolomerous type, together with imperfect remains of two neural arches. The neural spine, as preserved, is low. The central elements have heights of 27-29 mm., i.e., considerably bigger than those of embolomeres of the *Cricotus-Archeria* size range. It is of interest that both intercentrum and pleurocentra are wide anteroposteriorly (about 15 mm.), and that — a most unusual condition — the intercentrum is as stout as the pleurocentra.

A further specimen which may belong here is American Museum of Natural History No. 6939, the mold of which shows remains of a large shoulder girdle (Fig. 15). A nearly complete left clavicle is present, seen from the dorsal surface. Its well

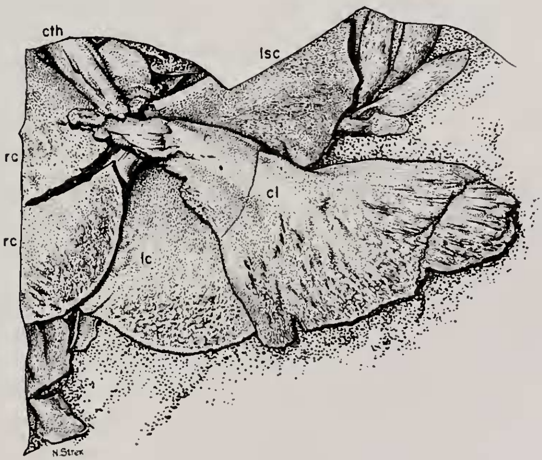

Figure 15. Shoulder girdle material from Linton. x½. Abbreviations: *cl*, left clavicle; *cth*, base of left cleithrum; *lc*, left coracoid plate; *lsc*, left scapular blade; *rc*, right coracoid plate.

developed acromial process lies to the left as the slab is figured; beyond it is the proximal part of the cleithrum. At the left of the slab is seen the inner surface of the right coracoid plate, showing its curved medial margin. Most of the left scapulocoracoid was present, but it is concealed in great part by the clavicle and right coracoid. Above the clavicle is part of the scapular blade: the upper part of the blade appears to have been broken off. Just above the edge of the clavicle there is a break in the thickened posterior rim of the blade, at about the summit of the supraglenoid buttress. Much of the left coracoid plate is visible between clavicle and right coracoid, and just below the stem of the clavicle can be seen part of the curved posterior margin of the subscapular fossa. Toward the upper right are embolomerous scales of appropriately large size.

A specific name for this Linton embolomere appears to be available. Newberry (1873, p. 342. pl. XXXIX, fig. 9) described as *Rhizodus lancifer* a large, incomplete tusk, striated proximally but smooth at the tip, from Linton. (The type specimen is Ohio State University No. 4500.) However, no identifiable crossopterygian remains of any sort have ever been discovered in the very considerable Linton materials. We are quite surely dealing with an amphibian tooth similar to the palatal tusks of the present animal.

Generic assignment presents an interesting problem. Most described embolomeres — including, for example, the Newsham specimens, *Pholiderpeton*, a small embolomere from Linton, and *Archeria* — have slender, closely spaced teeth, and with a high count of 40 or so in each jaw ramus. The only well known exceptions to this, apart from the form here considered, are the *Eobaphetes* jaw and the type of *Anthracosaurus russelli* from Airdrie, Scotland, originally described by Huxley (1863) and refigured by Watson (1929). *Anthracosaurus* and the present form appear to be almost identical in dentition, with powerful marginal teeth and palatal tusks, and with a low tooth count. In past times one hesitated to assign Paleozoic continental vertebrates from North America and Europe to a common genus, because of the supposed vast distance between the two regions. However, due to continually increasing evidence that in the Paleozoic those two areas were part of a common land mass and increasingly strong suspicions that the Atlantic sea barrier was then absent or negligible, I feel no hesitation in assigning this Linton animal to Huxley's genus, as *Anthracosaurus lancifer*

(Newberry). One possible bit of evidence to the contrary is that in the fragment of a large embolomere vertebral column from Linton, described above, the intercentrum is unusually broad, whereas in a series of large vertebrae from Airdrie (Museum of Practical Geology no. 56580-81) the intercentrum is of the more usual slender type. But since there is no certain association of vertebrae with skulls in either case, this need not be considered too seriously.[1]

The discussion of nomenclature above is based on the assumption that the large Linton embolomere is distinct from *Leptophractus obsoletus* from the same locality, the type of which is a much smaller individual with teeth which appear to be of a more slender, recurved and closely crowded nature. Should, however, the *obsoletus* type, on further study, appear to be a growth stage of the larger form, it will be noted that *Anthracosaurus* (Huxley 1863) and *lancifer* (Newberry 1856) have priority over *Leptophractus* and *obsoletus* (Cope 1873).

The Linton cannel is associated with the Upper Freeport Coal at the summit of the Allegheny series, to be correlated in age with the latest Westphalian D. *Anthracosaurus lancifer* is thus somewhat later in time than any of the described British embolomeres, although earlier than *Neopteroplax conemaughensis*.

Conemaugh series, Ohio. Apart from the *Neopteroplax* specimen, the only indication of a large embolomere from the Conemaugh is a single centrum (MCZ 2409) with a width of 36 mm., collected by Dr. and Mrs. Baird northeast of Reeds Mills, Section 36, Cross Creek Township, Jefferson County, Ohio. The horizon is that of the Summerfield limestone of the Conemaugh, equivalent to about the middle of the Stephanian. The size is appropriate for *Neopteroplax*, the type of which comes from a somewhat lower Conemaugh horizon.

Virgil series, Kansas. Williston in 1897 described a large labyrinthine tooth collected near the Vermillion River east of Louisville, Pottawotamie County, Kansas; the horizon is the Waubansee group at the top of the Pennsylvanian. The tooth is surely a palatal tusk of a large labyrinthodont, but it is impossible to say whether embolomere or temnospondyl.

Late Pennsylvanian and earlier Permian of Texas. The typical — and so far the only identified — Permian embolomere is

[1] Note that in the case of both Airdrie and Linton skulls we cannot be certain that we are actually dealing with true embolomeres, although both are quite surely anthracosaurians of some sort.

Archeria (formerly called "*Cricotus*"). This is (except in late horizons) a small form, with vertebral centra generally averaging little over 20 mm. in diameter. Some years ago, while exploring low horizons in the Permian which are close to the Carboniferous boundary and were formerly considered Carboniferous in age, a party from this museum discovered a "pocket" in southeastern Archer County filled with disarticulated and generally weathered bones and bone fragments. This "Prideaux pocket" lies in the valley of the West Fork of the Trinity River, in Section 1, IRR Co. Survey, Abstract 2237. The local stratigraphy is poorly known, but the locality is probably in the Pueblo formation, close to the base of the Wichita group and not far above the summit of the Pennsylvanian as currently defined in this region. Mingled with elements pertaining to pelycosaurs and the typical rhachitome *Eryops* as well as unidentifiable scraps, are numerous small centra and intercentra, with diameters averaging 22 mm., surely pertaining to *Archeria.* But present as well are a few much larger embolomerous central elements (MCZ No.

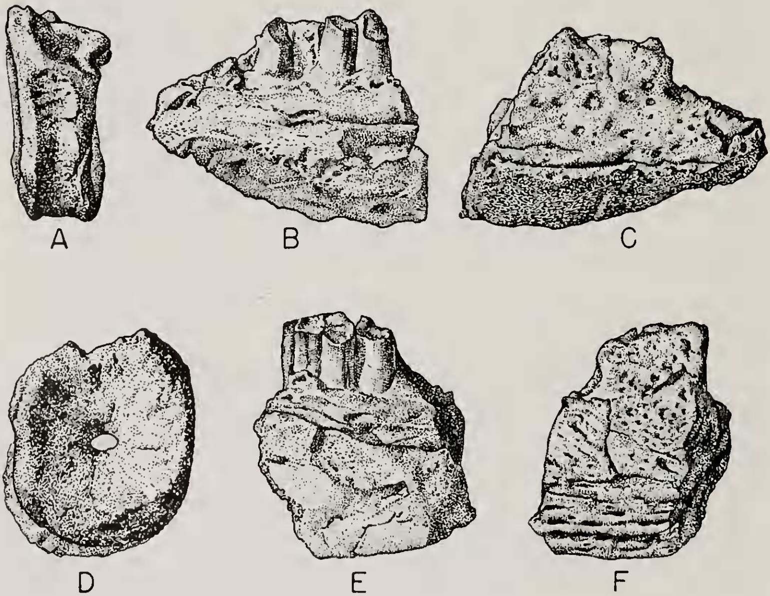

Figure 16. Type materials of *Neopteroplax relictus* sp. nov. *A, D,* centrum in lateral and anterior views; *B, C,* and *E, F,* two jaw fragments in internal and external views. x⅔.

2237) with diameters of approximately 40 mm. We have here, it would seem, the last survivor of the large embolomeres of the Carboniferous.

After the main body of this paper had been completed, some further light was shed on the matter by the discovery, by Mr. Gene Wilson of Ringgold, Texas, of fragmentary remains of a seemingly comparable amphibian at a still lower horizon. The materials (MCZ 2353) include several central elements similar in size to those from the "Prideaux pocket" and two jaw fragments (Fig. 16). The teeth, although broken at the tips, show the close-set pattern seen in *Neopteroplax;* they are transversely oval in section at the level of the outer margin of the dentary, with dimensions of 5½ by 6 to 8 mm. This form can be reasonably interpreted as a surviving member of the genus *Neopteroplax.* Geological and geographical considerations make it unlikely that it is specifically identical with the Ohio Conemaugh form, and despite the fact that no diagnostic features can be named other than the somewhat larger average size of centra and dentary teeth, the new materials are here designated as the holotype of *Neopteroplax relictus,* sp. nov. They were found in shales a few feet below a small outlier of the Blach Ranch Limestone, 2½ miles north and ½ mile east of Graham, Young Co., Texas. The Blach Ranch lies in the Thrifty Formation of the Cisco group; despite the fact that there has been a trend in recent decades for a downward shifting of the Pennsylvanian-Permian boundary in this area of Texas, it is still almost universally agreed that the Thrifty Formation is definitely pre-Permian (and pre-Wolfcamp) in age.[1]

SUMMARY

The skull of a large embolomerous labyrinthodont from the Conemaugh group in Ohio is described as *Neopteroplax conemaughensis,* gen. et sp. nov. Other remains of large American embolomeres are reviewed, including *Pholiderpeton? bretonense* from the Point Edward formation of Nova Scotia; *Eobaphetes kansensis,* which appears to come from the Morrow series in Arkansas rather than Kansas; the problematical *Eosaurus acadianus* and "*Baphetes*" *minor* from the Joggins exposures in Nova

[1] I wish to thank Dr. Walter Dalquest of Midwestern University, Wichita Falls, Texas, for bringing Mr. Wilson's find to my attention, and Mrs. Ida Mae Fletcher and Mr. and Mrs. Richard Layfield of Graham for their courtesies during a trip to the site of the discovery.

Scotia; skull and other materials from the Conemaugh of Linton, Ohio, here termed *Anthracosaurus lancifer;* large vertebrae and jaw fragments from the late Pennsylvanian and earliest Permian of Texas named *Neopteroplax relictus* sp. nov.; fragmentary remains from several additional Pennsylvania localities and horizons.

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